SAP PRESSURE IN THE BIRCH STEM

PART I

H. E. MERWIN AND HOWARD LYON

(WITH FIVE FIGURES)

During the seasons of 1902 to 1904 sap pressure observations were made on several kinds of trees in the vicinity of Oneonta, in central New York. Birches and maples illustrate the two extreme types of sap pressure phenomena. Our observations on the maples are in accord with those of other observers, especially as set forth by JONES, EDSON, and MORSE.[1] Sap pressure in the birches has not been studied much hitherto, except as incidental to other studies.

We found that glass tubes of small bore filled with mercury made very sensitive pressure gauges, especially if the tap hole in the tree and the connecting tubes were filled with water or sap when the gauge was attached. When pressure was negative (suction), a bulb tube was sometimes arranged to allow water to flow into the tap hole, and to catch the gas which escaped. Gas in the tap hole when pressure is negative causes disturbing capillary effects. Gas in the tubes has a damping influence upon the gauge.

Characteristics of sap pressure in the birches

No sap will flow from tap holes in the stem of the birch or ooze from cut twigs till the ground has thawed considerably in the spring. It is not necessary, however, that the air temperature be continuously above the freezing point before pressure becomes high. From April 5 to April 22, 1904, we have recorded seven nights in which the temperature was below freezing; yet on April 5 a positive tension of 44.3^{cm} was observed in a yellow birch (*Betula lutea*); April 9, 87^{cm} in a black birch (*Betula lenta*); April 18, 35^{cm} in a black birch. Freezing nights were often accompanied by negative pressure which was maintained for a few hours after sunrise. The maximum pressure comes about a month after the first decided appearance of pressure. The buds by this later time have begun to unfold. There is at all

[1] JONES, C. H., EDSON, A. W., AND MORSE, W. J., The maple sap flow. Vt. Agric. Exper. Sta. Bull. 103. 1903.
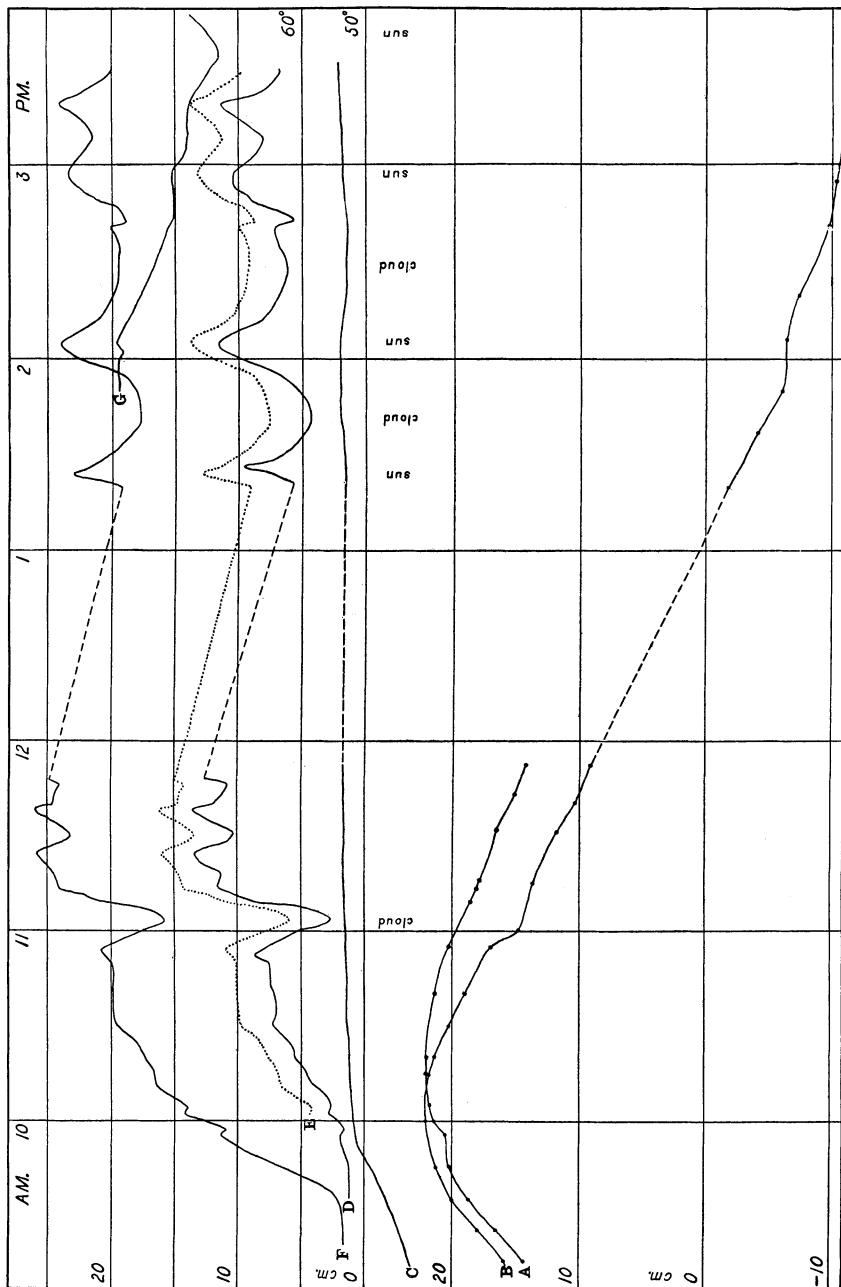
FIG. 1.—Sap pressure curves for maples and birches April 18, 1904: *A*, near the base of a 12-inch maple; *B*, 157cm above *A*; *C*, the shade temperature; *D*, 180cm from the base of 7-inch black birch; *F*, 135cm below *D*; *E* shows where the pressure curve of *D* would have been if there had been exact hydrostatic equilibrium within the tree; *G*, curve for a 10cm maple; the responses of pressure to sunshine and cloud are to be noted.

times a very regular distribution of pressure in the birch trunk, taps
at the same height giving like pressures, and taps at different heights
showing most pressure in the lowest. The difference between the
pressure in the lowest tap hole and that in the highest is usually
slightly greater than the hydrostatic difference in level between the
holes (*fig. 1*).

Pressure in one hole is always immediately and markedly lowered
by sap flowing freely from another hole, even though the holes are
on opposite sides of the tree and many feet apart vertically. This
fact, of course, indicates a free intercommunication among the ducts
of the birch wood.

In all of the cases we have observed, pressure began to be evident
at the base of the tree first, and as pressure increased there it showed
itself higher and higher up.

Daily fluctuations of pressure in the birch were reported by CLARK.[2]
The general character of these fluctuations was brought out by our
observations in April 1904. A rapid rise of pressure beginning in
the morning is followed by a slow decline till near sunset, then a
gradual rise is kept up during the night. The nightly rise of pressure
is checked if the temperature of the tree falls below freezing. Changes
of pressure are only slight the next day after a freezing night, unless
the air temperature reaches 40° to 45° F. or more. (These oscillations
of pressure occupying a period of a day are graphically shown in *fig. 3*
of the second part of this paper.)

The most striking phenomenon of the birch sap pressure is its
variability during those rapid changes of sunshine that take place on
days when cumulus clouds occasionally drift before the sun. We
have seen the mercury column in a gauge move more than 2.5^{cm}
vertically in a minute in response to a change of less than 1° C. as
registered by a blackened-bulb thermometer exposed to the sun.
Furthermore, pressure changes of this rapidity have been kept up
for nearly ten minutes at a time. *Fig. 2* is a record for part of an
afternoon in which bright sunshine and dense cloud-shadow alter-
nated. A drop in pressure of 37.5^{cm} of mercury during a period of
cloud-shadow, and a subsequent rise of 30^{cm} when the sun appeared,
took place between 2:30 and 3:20 P. M. A comparison of the birch

² CLARK, W. S., The circulation of sap in plants. 1874.

with the maple, in respect to pressure and the passing of clouds, may be made from *fig. 1.* Even the most decided ups and downs in the curve of the birch pressure are scarcely more than suggested by the slight steepenings or flattenings in the long slopes of the maple curve.

We have always found the maximum pressures in large birches higher than in small ones. The highest pressures observed in both large and small trees were on May 2, 1904. A 7.5^{cm} black birch then gave a record of 91^{cm} (1.2 atmospheres), a 17.5^{cm} black birch of 146^{cm} (1.9 atmos-pheres), and a 35^{cm} black birch, about 20^m high, the astonishing pressure of 204^{cm} (2.68 atmospheres). The last pressure would doubtless have been even greater if it had been taken two hours earlier, for both the 7.5^{cm} and the 17.5^{cm} trees had already declined more than 10 per cent. from maximum when the large tree was tapped. As it is, this pressure is equal to 200^{cm} of mercury or 27^m of

FIG. 2.—The intensity of the sunshine as measured by a blackened-bulb thermometer and the concurrent pressure, measured in inches of mercury, at the base of a 35^{cm} black birch, May 2, 1904.

water, being 1.8^m of water higher than any previously recorded sap pressure (CLARK, *l. c.*) Such pressure would support a column of water 7.8^m higher than the tree. The highest point on the pressure curve of *fig. 2* represents this pressure.

Negative tensions occur frequently in the higher parts of the trunk of the birch, and less frequently near the base. In the latter position it is only in the early part of the season that suction is kept up for more than a few minutes at a time. On April 22, 1904, suction pre-vailed all day in yellow and black birches that had been in states of

high pressure on several occasions since April 5. A hard freeze the night before and a temperature not exceeding 40° F. during the day seem to have been the chief factors controlling the negative pressure.

The chief characteristics of sap pressure in the maple

On some warm winter days, at least as early as February 1, sap will flow in amounts of a few cubic centimeters from tap holes in small maples that are exposed to the sun; but the maximum flow and corresponding pressure do not occur till the ground is thawing in the spring. At this time pressures in a tree are not distributed with any apparent regularity. Portions of the trunk at the same level may give very different pressures, and for different heights the pressure may be greatest in either the highest or the lowest situation, though usually pressure decreases irregularly with height (*fig. 1, A* and *B*).

Pressure in one tap hole may be but little decreased by sap flowing freely from another hole a few inches at one side of it, but there may be a decided drop in pressure if the flow is from a hole a few feet above or below the hole to which the gauge is attached. From these facts it may be inferred that the ducts of the maple communicate with some freedom along the grain of the wood, but scarcely at all across the grain.

When pressure begins it may be manifest first either near the roots or in the branches, but for any given place in the trunk there is a strong tendency toward a daily increase of pressure during the morning hours, and a decrease during the afternoon. The decrease often goes beyond zero to a considerable suction (*fig. 1, B*, after 1:00 P. M.). Size of the tree, situation, and depth of tapping all affect the character of the daily pressure variation. Small size, exposure to the sun, and shallow tapping are all favorable to extreme and rapid pressure changes. In spite of all the variations already discussed, there is a tendency toward parallelism of the pressures developed in different parts of the same tree, and in various trees during a daily period. The causes of such pressure variations, as related especially to daily periods of temperature change, have been discussed by various writers.

There is a general agreement that rises and falls of temperature

of a few minutes' duration have almost no effect upon pressure in the maple.   The Vermont *Bulletin* records one instance when a wavy line given by a recording gauge was probably due to variations in sunlight, pressure falling slightly when a cloud obscured the sun. Our record of April 18, 1904, shows conclusively that maples may respond notably to variations in sunlight.   In *fig. 1*, lines *A*, *B*, *G* are pressure curves for maples.   At 11 A. M. and at 2:00 and 3:35 P. M. the irregularities in the curves were observed to be directly related to insolation.   As to the amount of tension that has been observed in maples, our highest records were from a 25^{cm} tree March 12, 1902, 75^{cm}, and from a 10^{cm} tree April 5, 1904, 69^{cm}.   The Vermont *Bulletin* (p. 75) records a pressure equal to 129^{cm} on March 21, 1898.   Pressures exceeding 75^{cm} are only occasionally observed. Negative pressures seldom exceed 20^{cm}.

PART II

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Causes of sap pressure variations in the birches

The studies of 1906–1908 were carried on in Cambridge, Mass., in the hope of getting more data as to the causes of pressure variations in birches.

The character of both the long and the short period oscillations on the pressure curve, and the corresponding record of a freely exposed blackened-bulb thermometer for several days, are shown in *fig. 3*. Several important relations are to be noted between the two curves. During the day there is a close parallelism; at night the pressure curve rises regardless of temperature.   In other words, maximum pressure and maximum insolation occur at about the same time, near the middle of the day; but minimum pressure comes near sunset, while minimum temperature is nearly 12 hours later, shortly before sunrise.   Some of the factors in the control of sap pressure are brought out in the several experiments and discussions that follow.   The details of the longer experiments referred to in the general discussion are given under a later heading.

Experiment shows that during the sap season for the birch, all the intercommunicating cavities of the roots and stem are kept practically full of sap.   One tree (*exp. 1*) gave the calculated gas
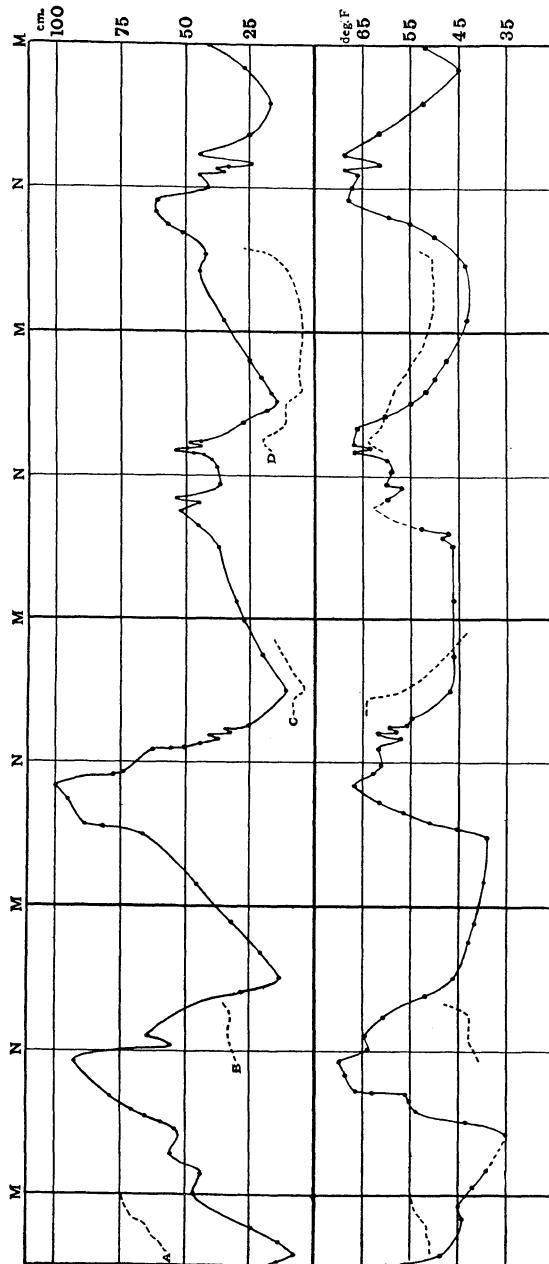
FIG. 3.—The upper curves are the records of pressure in a white birch 11cm in diameter; the continuous line covers the period April 18–21, inclusive, 1906; and the dotted lines *A*, *B*, *C*, *D* are partial records for April 14, 23, 28, 30 respectively; after April 18 the pressure was somewhat lower than it would otherwise have been, owing to a continuous slight flow of sap from the tree; the lower curves are temperatures in the sun; *M*, midnight; *N*, noon.

content of the vessels as about 1 per cent. of the total volume of the vessels.   This fact easily explains the state of hydrostatic equilibrium which observation shows to exist in the birch stem when pressures are high.   Increasing pressure must diminish the size of gas bubbles to a considerable extent by increasing the solubility of the gas in the sap; decreasing pressure would have an opposite effect.

There is, however, until rather late in the sap season, a good deal of gas in the closed cavities of the wood fibers.   This is shown by specific gravity tests.   A density of 1 is not attained in the wood of the branches until the buds are about one-third longer than in their winter condition.   The maximum density of 1.14 to 1.17 is reached when the first leaves are about 8^{mm} long, near the end of the sap season.   About a month is required for an increase of 25 per cent. in density.   Therefore, the aerial parts of the tree considered in *exp. 1*, with an estimated volume of 57,000^{cc}, would require about 500^{cc} of water as a daily supply from the roots to bring about this increase in density.

To get an idea of the amount of water required to maintain evaporation from a tree at the middle of the sap season, two twigs, weighing 1.94^{gm} and 2.3556^{gm} respectively, after the cut ends had been sealed with balsam were exposed for 3 hours, the first to a temperature of 70° F. in the laboratory, the second to about 42° F. in a breeze. The first twig lost 0.0381^{gm}, and the second 0.0256^{gm}.   An average evaporation of 0.01^{gm} per hour for a twig weighing 2^{gm} may be taken, therefore, as an approximate measure of evaporation from the birch for the middle of the sap season.   The tree of the experiment bore about 2000 such twigs, from which the evaporation at this rate would be 480^{cc} of water per day.

This water evaporated from the tree and that absorbed by the wood fibers during the increase of density of the tree may be taken as the approximate amount of water supplied to the tree daily by root absorption.

Inasmuch as pressures are freely transmitted throughout the birch stem, it is evident that *variations in the rate of evaporation and infiltration and of root absorption*[3] *will cause variations in pressure.*

3 LIVINGSTON (The rôle of diffusion and osmotic pressure in plants. 1903) has discussed the factors concerned in the control of absorption and pressure in roots.

It is needless to enumerate the weather conditions which affect the rate of evaporation, but it is worth while to note at least one chief factor in the control of root absorption.   It is well known that root absorption is accelerated by moderate increase of ground temperature above the freezing point.   It has been shown by MacDougal[4] that ground temperatures in the vicinity of New York City at a depth of 30^{cm} are maximum about 8:00 to 11:00 at night, and minimum about 8:00 to 10:00 in the morning.   At greater depths the maximum and minimum would occur later, but the temperature variations would be less marked.   Therefore the maximum temperature of the roots of birches—which lie mostly within less than 60^{cm} of the surface of the ground—must occur during the night, and the minimum temperature during the afternoon.   Thus, root absorption and the pressure produced by it tend to increase at night.   In Clark's (*l. c.*) experiments on roots severed from the tree, the rule was for root pressure to increase during the night and decrease during the day, for the whole period in which pressure was strong.

Taking the combined effect at night of increasing root absorption and decreased evaporation, there is a decided tendency toward an increase of pressure in the stem during the night.   As the pressure increases the rate of infiltration also increases, tending thus to diminish the rate of increase of pressure (*fig. 3*).   After sunrise evaporation begins to oppose the rise of pressure, so that about noon pressure begins to decline.   The decreasing activity of the roots at this time aids the decline.   What pressure might be developed in a birch stem by the prolonged action of root pressure, if the modifying influences of evaporation and infiltration could be eliminated, is shown by Clark's record of 193^{cm} pressure in a birch root severed from the stem.   This pressure is more than double the pressures usually observed in the trunk.

Assuming that root pressure is essentially osmotic, the concentration of the sap in the root Clark observed must have been about two and a half times that of the sap at the bases of trees I have observed. At different times during the sap season, I have evaporated sap from birches and found it to contain 0.5 to 1 per cent. of solids, largely

4 MacDougal, D. T., Soil temperatures and vegetation.   Monthly Weather Review **31**:no. 8. 1903.

glucose.   A sap containing o.8 per cent. of glucose represents an osmotic pressure of about 78^{cm} at o° C.   It follows, then, that 100^{cm} of pressure in a birch stem is the maximum to be expected from root pressure.

Volume changes in the sap and wood due to changes of temperature in the tree cause marked variations in pressure.

I find that the expansion of sap from 6° to 32° C. is only 2 per cent. greater than the expansion of water.   Cell wall substance, on the other hand, when saturated with water, expands about 2.2 times as much as water between 6° and 32° C. (*exp. 3*).

Observations as to the elasticity to the transmission of light of birch wood tissue in a thin microscopic section shows that wood fibers and the walls of the vessels in the wood have the least elasticity parallel to the length of the stem, and that the medullary rays have least elasticity along radii of the stem.   In a wood fiber the greatest elasticity is perpendicular to the surface.   By comparison with other substances, in which expansion by heat is directly related to elasticity to light, a different coefficient of thermal expansion for different directions would be expected in both single wood fibers and in masses of wood.   My determinations made on strips of green white birch wood about 500^{cm} long immersed in water show that between 6° and 32° C. there is contraction instead of expansion in a radial direction when the temperature is raised.   Under like conditions a longitudinal strip showed at first a slight expansion, but in two subsequent determinations it contracted.   The coefficients of radial contraction obtained were o.000005, o.000004, and o.000006; and those of longitudinal contraction were o.000002 and o.000003.   These coefficients are so extremely small that they may be neglected in the following sap pressure calculations.[5]   It thus appears that the volume changes in the cell walls above mentioned are made possible only by a diminution of the area of cross-section of the vessels and of the cavities in the cells, for the external dimensions of the tree change scarcely at all.

The effect of this tendency to diminish the pore space in the wood

[5] The thermal expansion—based upon *exp. 3* and upon the above coefficients— of a given volume of birch wood, of which 40–45 per cent. is saturated cell wall, amounts to about 1.5 times the expansion of an equal volume of water.

is to produce pressure on the liquid or gas occupying the pores.   If liquid alone completely filled the cavities of the wood, any amount of thermal expansion would necessarily be accompanied by an equal amount of elastic expansion of the wood.   Pressure in this case might be very great.   It should be noted, however, that the pressure recorded by a gauge would be less than that developed in the tree without the attached gauge, for the sap forced from the tree into the gauge would partly relieve the pressure within the tree.   It follows that the less the amount of sap required to operate a pressure gauge, the higher the pressure it will record for a given amount of thermal expansion within the tree.

It probably never happens that the wood of a birch tree becomes completely saturated with water.   One or two per cent., at least, of gas is present in the wood fibers when the wood is densest.   A smaller amount is present in the vessels.   The compressibility of this gas lessens the effect of thermal expansion in producing pressure.

In order to obtain a quantitative statement of the amount of thermal expansion, I have made the following estimates.   The small white birch (11^{cm} diameter) of *exp. 1* has about 10 per cent. of its volume in small branches and twigs.   These must vary in temperature in the same way that a blackened-bulb thermometer would, only in a less degree—say a maximum daily range of 20° C.   The trunk would vary less in temperature than the air—say 10° C.   The maximum daily change of volume of the sap and cell walls of the tree computed on this basis would be 270^{cc}, or nearly 0.5 per cent. of the volume of the tree.   Under such conditions the presence of as little as 1 per cent. of gas in the vessels would prevent an existing small pressure from rising more than about 40^{cm}.   The slight increase of pressure due to the greater expansive force of the gas at the higher temperature is so small that it may be disregarded.

We may now consider in detail some of the instances in which temperature controls pressure by causing volume changes within the tree.   *Fig. 2* is a record of pressure, and of temperature as given by a blackened-bulb thermometer.   The periods of lower temperature were caused by the passing of clouds.   Pressure increased during the periods of sunshine and diminished during the intervals of shadow. From 3:00 to 3:20, while the sun shone bright, the temperature of the

thermometer increased 7° C.   The corresponding increase in pressure was 30^{cm}.   It is impossible that any part of the tree except the smallest twigs could have been heated during so short a time more than 3 or 4°.   There must have been, therefore, little or no gas in the vessels of the tree.

On April 21, 1906, from 2:00 to 2:45 P. M. (*fig. 3*), a rise of temperature of 4°.5 C. was accompanied by an increase of pressure of 20^{cm}.

At sunrise on each of the mornings included in *fig. 3* the pressure curves steepen greatly.

During the afternoon of April 23, 1906 (curve *B*, *fig. 3*), the pressure was rising slowly till nearly sunset in response to a change of the weather with rising temperature.

From the foregoing discussions it may be reasonably inferred that there are two chief pressure-producing agencies concerned in the phenomenon of sap pressure in the birch stem, namely root pressure and thermal expansion.   The effects of both are modified considerably by evaporation and by infiltration of sap into the wood cells. Root pressure and evaporation produce a daily oscillation of pressure, with the maximum shortly after sunrise and the minimum at sunset. Thermal volume changes in the tree cause a rise of pressure from sunrise till shortly after midday, and a fall from then till sunrise. Irregular minor oscillations of short period are caused by corresponding changes in air temperature or brightness of sunshine.   The combined effect of the two agencies is to make the observed maximum come about midday and the minimum at sunset.   The maximum is somewhat higher than would be produced by root pressure alone— in extreme cases twice as high.

If a tree is tapped when the pressure is high, the flow of sap is at first copious, but the rate of flow lessens rapidly.   The pressure, as measured anywhere in the trunk, also declines (see *exp. 2* and *fig. 5*). The relation of pressure to flow during this period of falling is different for different relative positions of the gauge and the flowing orifice. Taking a theoretical case, the pressure as distributed over a radial section of a tree before tapping is represented in *A*, *fig. 4*.   Lines of equal pressure are horizontal, and pressure increases downward. Shortly after tapping at *a*, the lines of equal pressure are as shown in *B*.   A little later they are as in *C*.   (The diagrams are constructed

for a case in which the resistance to flow of sap is twice as great radially as longitudinally.)

Now let the rate of flow for the first ten minutes after tapping be represented by *fig. 4, D,* curve *N,* and let *B* show the distribution of pressure at the end of two minutes, and *C* at the end of the 10 minutes. Let the pressure be measured at the three points x, y, z. The pressure in x before tapping is 40.5^{cm}, at the end of 2 minutes it is 35^{cm}, and at the end of 10 minutes it is 25^{cm}. These values are plotted in *fig. 4, D,* curve *X.* The values for the pressure in holes y and z are likewise plotted in *fig. 4, D,* curves *Y* and *Z.* Inspection of these
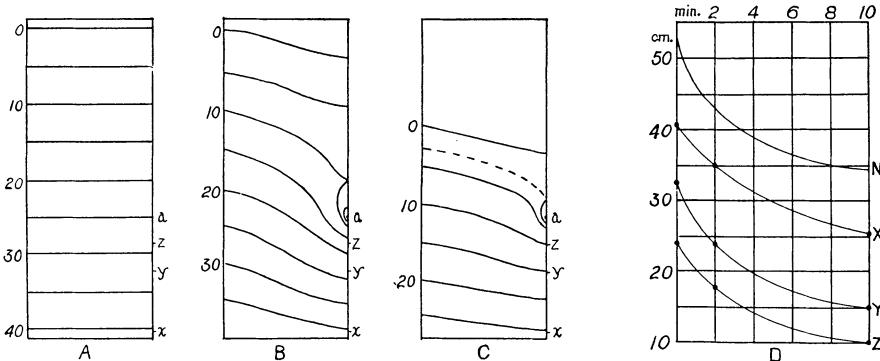

FIG. 4.—For explanation see text.

curves of pressure and the curve of flow shows that there is no definite general relation between pressure and flow.

Experiments

EXPERIMENT I.—During the evening of April 14, 1906, while the normal evening rise of pressure was in progress, a white birch (*Betula populifolia*) 11^{cm} in diameter and 6^{m} high was tapped for two gauges 157^{cm} vertically apart. The pressure from the first was more than enough to sustain a column of water as high as the tree. The difference in pressure of the two gauges was 12 to 12.3^{cm} of mercury, the hydrostatic pressure corresponding to this difference in the height of the two gauges being 11.6^{cm}. This hydrostatic equilibrium may be explained on the supposition that a practically continuous column of water could have been traced through at least some of the ducts between the tap holes. Other ducts might have contained bubbles

of gas.   That there was a small amount of gas present was shown by pouring mercury into the free arm of the lower gauge and thereby forcing back into the tree 0.45^{cc} of sap.   This procedure caused the pressure within the tree to go up from 54 to 55.3^{cm}.   A simple calculation shows that there was a contraction of nearly 1 per cent. in the gas in the vessels.   The total volume of gas contracting was then 45^{cc}.

To get an estimate of the amount of duct space in the tree, I examined several cross-sections of branches about 2.5^{cm} in diameter. An area of 1.25$^{sq\ mm}$ contained an average of 74 ducts, with an average cross-section of 0.002$^{sq\ mm}$.   The ducts, therefore, occupy about 12 per cent. of the volume of the tree.   The volume of the tree (estimating the upper 3^{m} of the stem and branches as equal to the lower 3^{m} of the trunk) was 57,000^{cc}.   The duct space, then, amounted to about 6800^{cc}.   Finally, 45^{cc} (the gas content of the ducts) is nearly 0.7 per cent. of the volume of the ducts.   A second addition of mercury gave the gas content as 1.3 per cent.   The ducts, therefore, at this time of the year were almost entirely filled with water.   In a larger tree, in which there is a good deal of heart wood, there might be considerably more gas in the ducts, but many of the ducts in the heart wood are probably not freely communicating with the ducts in the sap wood.

It was noticed in connection with adding the mercury to the gauge, that after the rise of pressure thus produced had taken place, the pressure remained stationary for 15 minutes the first time, and for 30 minutes the second time, and then began rising at its previous rate. Furthermore, the length of time that pressure was stationary was such that during that time pressure would have increased naturally the same amount that it was artificially raised.   We may conclude from this that the *intensity* of root pressure was increasing during the night.   This is in accord with the idea that the concentration of the sap in the roots—and the corresponding osmotic pressure—becomes greater when evaporation from the branches lessens.

EXPERIMENT 2.—Before sunrise April 16, 1906, when pressure was high and slowly rising, three holes were bored in a small birch trunk, about 1.5^{m} apart vertically.   Gauges were attached to the lower holes and the upper one was plugged.   Equilibrium was soon established between the gauges, the upper one reading 61.9^{cm} and the

lower one 76.3^{cm}.   The difference (14.4^{cm}) is 2.8^{cm} more than the
pressure of the sap column between the holes.   This is the condition
that would obtain if sap were being artificially pumped into the base
of the stem and were evaporating slowly from the top.   Friction of
the sap in the ducts would cause the lower gauge to read higher than
if no current were flowing.

The gauge in the middle hole was then removed and the sap
allowed to flow from the hole.   A few minutes later the upper hole
was unstopped, but no sap flowed from it, though sap had flowed from
it when the hole was made.   The flowing of the hole below it had
caused it to cease to flow.   As soon as the middle hole began flowing,
the pressure in the lower hole dropped rapidly to 23.4^{cm}, and there
remained nearly stationary for over an hour.   The total drop in
pressure in the lower hole was thus 52.9^{cm}, but in the hole above the
drop was 61.9^{cm}.   In other words, the pressure in the lower hole
was 11.8^{cm} more than enough to raise sap to the level of the flowing
hole.   This, also, is a condition to be expected if a current of sap was
flowing upward from the roots through the stem, overcoming friction.

The flow from the middle hole was at first rapid—17 drops in
10 seconds—but it decreased in a few minutes to 8 drops per 10
seconds, and at the end of 20 minutes to 4 drops.   The flow then
continued at nearly this rate for more than an hour.   Curves *A* and
B, *D* and *E*, of *fig. 5* are plotted from these observations.   Curve *C*
shows the drop of pressure from a similar experiment on another tree.
Although the curves are nearly parallel, the ratio of flow to pressure is
greater for the highest pressure than for the lowest.   This relation
may be explained by assuming that the copious flow of the first few
minutes had a double source of supply;   the larger part came from
the trunk, being forced toward the tap hole by the elastic expansion
of the wood and the gas in the wood;   and the smaller part came as a
current from the roots.   As soon as the excess of pressure in the stem
had been relieved, the further and nearly uniform flow was kept up by
the root pressure.   Changes in the degree of cloudiness produced
the waviness of the curves *C*, *D*, and *E* in *fig. 5*.

During the 20 minutes that the flow was decreasing 790 drops
(66^{cc}) of sap escaped.   Of this not more than 40^{cc} or less than 25^{cc}
could have come from the roots.   (This will be seen by a study of

curve *B*.)   Therefore, 32^{cc} is close to the amount supplied by the roots and therefore about 34^{cc} came from expansion within the tree.   The experiment of two days before showed the amount of gas in this tree to be 45 to 80^{cc}, an amount which, by expansion, is sufficient to account for the flow here considered.
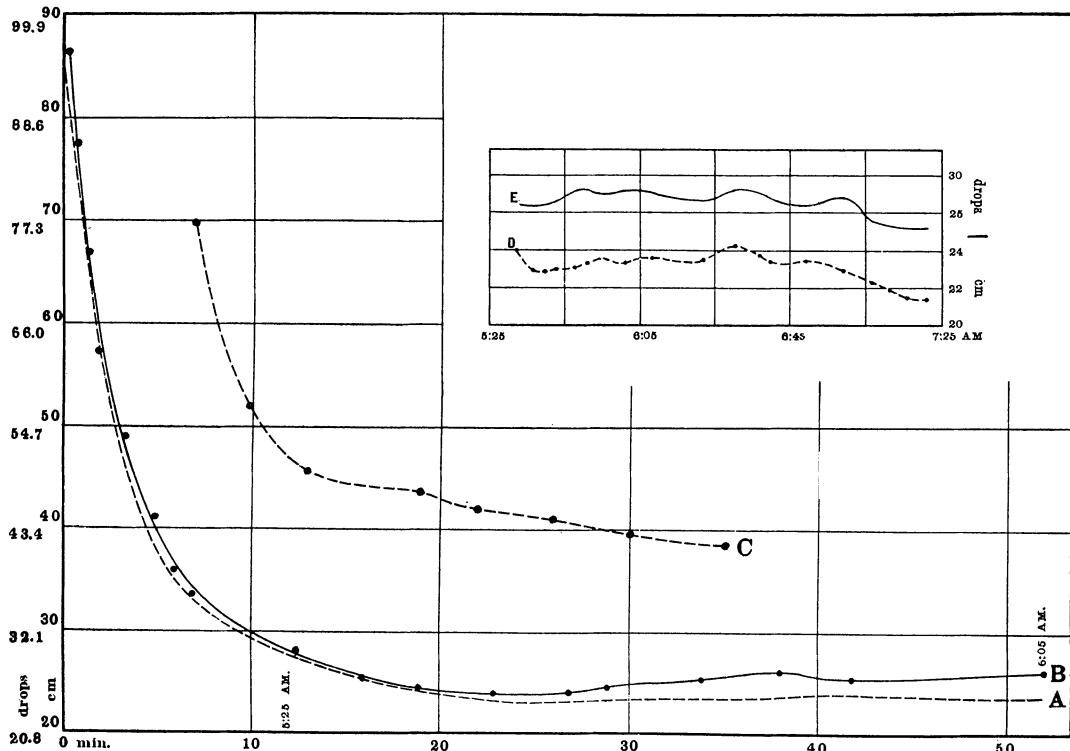

FIG. 5.—*A*, pressure at the base of a white birch, April 16, 1906, while flow was taking place from a hole higher up; *B*, rate of flow in drops per minute of the hole above *A;* the continuation of curves *A* and *B* are *D* and *E;* in another tree the decline of pressure while sap was flowing freely is shown by *C*.

EXPERIMENT 3.—To determine the amount of expansion of saturated cell-wall substance of birch wood.

Across the grain of a white birch plank thin shavings were taken. From these the air was entirely expelled under the receiver of an air pump.   The shavings were then transferred to a 100^{cc} pycnometer. The pycnometer was filled up with freshly boiled, distilled water, and weighed at 6° C., and again at 32° C.   The weight of the pycnometer

full of water alone was also taken at these temperatures. Finally the weight of the completely dried shavings was found. Now the specific gravity of dry cell wall substance is approximately 1.56, and the volume of saturated cell wall substance is nearly 3/2 that of dry cell wall substance.[6]   Then let $a=$ increase in weight of pycnometer full of water from 32° C. to 6° C.; $b=$ increase in weight of pycnometer full of water and shavings from 32° C. to 6° C.; $c=$ increase in volume of pycnometer from 32° C. to 6° C.; $d=$ volume of pycnometer; $e=$ volume of saturated cell wall substance; 0.0046 = expansion of 1^{cc} of water from 6° C. to 32° C.   Then

$$\frac{b+c-(d-e)\left(\dfrac{a+c}{d}\right)}{e\times 0.0046}$$

= the ratio of expansion of cell wall to the expansion of water from 6° C. to 32° C.[7]   Now, by substituting the values obtained in the experiment,

$$\frac{0.4975+0.066-(100-12.6)\left(\dfrac{0.433+0.066}{100}\right)}{12.6\times 0.0046}=2.2$$

= the desired ratio of expansion.

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[6] These are the figures given by SACHS, HARTIG, and others, and used in compiling the tables of the Vermont *Bulletin*.

[7] This formula would need slight corrections for more exact work, but it is more accurate than the factors of specific gravity and volume of saturated cell wall.